



THE UNIVERSITY *of* EDINBURGH

## Edinburgh Research Explorer

### Parental care buffers against inbreeding depression in burying beetles

**Citation for published version:**

Pilakouta, N, Jamieson, S, Moorad, J & Smiseth, PT 2015, 'Parental care buffers against inbreeding depression in burying beetles', *Proceedings of the National Academy of Sciences (PNAS)*, vol. 112, no. 26, pp. 8031–8035. <https://doi.org/10.1073/pnas.1500658112>

**Digital Object Identifier (DOI):**

[10.1073/pnas.1500658112](https://doi.org/10.1073/pnas.1500658112)

**Link:**

[Link to publication record in Edinburgh Research Explorer](#)

**Document Version:**

Publisher's PDF, also known as Version of record

**Published In:**

Proceedings of the National Academy of Sciences (PNAS)

**General rights**

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

**Take down policy**

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact [openaccess@ed.ac.uk](mailto:openaccess@ed.ac.uk) providing details, and we will remove access to the work immediately and investigate your claim.



# Parental care buffers against inbreeding depression in burying beetles

Natalie Pilakouta<sup>1</sup>, Seonaidh Jamieson, Jacob A. Moorad, and Per T. Smiseth<sup>1</sup>

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3FL, United Kingdom

Edited by Raghavendra Gadagkar, Indian Institute of Science, Bangalore, India, and approved May 19, 2015 (received for review January 12, 2015)

When relatives mate, their inbred offspring often suffer a reduction in fitness-related traits known as “inbreeding depression.” There is mounting evidence that inbreeding depression can be exacerbated by environmental stresses such as starvation, predation, parasitism, and competition. Parental care may play an important role as a buffer against inbreeding depression in the offspring by alleviating these environmental stresses. Here, we examine the effect of parental care on the fitness costs of inbreeding in the burying beetle *Nicrophorus vespilloides*, an insect with facultative parental care. We used a  $2 \times 2$  factorial design with the following factors: (i) the presence or absence of a caring female parent during larval development and (ii) inbred or outbred offspring. We examined the joint influence of maternal care and inbreeding status on fitness-related offspring traits to test the hypothesis that maternal care improves the performance of inbred offspring more than that of outbred offspring. Indeed, the female’s presence led to a higher increase in larval survival in inbred than in outbred broods. Receiving care at the larval stage also increased the lifespan of inbred but not outbred adults, suggesting that the beneficial buffering effects of maternal care can persist long after the offspring have become independent. Our results show that parental care has the potential to moderate the severity of inbreeding depression, which in turn may favor inbreeding tolerance and influence the evolution of mating systems and other inbreeding-avoidance mechanisms.

parental care | environmental stress | fitness | inbreeding depression | inbreeding tolerance

Inbreeding is an important issue in evolutionary biology and ecology because of its profound implications for genetic variation and the evolution of mating systems and reproductive strategies (1–5). Inbreeding results from matings between related individuals and can cause a reduction in offspring fitness because the higher degree of homozygosity associated with inbreeding increases the risk that deleterious recessive alleles are expressed (6). Evidence for such fitness costs of inbreeding, known as “inbreeding depression,” has been documented in a wide range of taxa, including mammals, birds, insects, and plants (7). However, there is substantial variation in the severity of inbreeding depression among species as well as among and within populations of a species (7–10). This variation may be driven in part by differences in the physical or social environment, which can have a major effect on the severity of inbreeding depression (11, 12). For example, environmental stresses such as starvation and competition are expected to exacerbate inbreeding depression (9, 11).

Parental care is an important component of the social environment in many birds, mammals, and insects (13). It is thought to have evolved as a means by which parents enhance their offspring’s fitness by neutralizing the detrimental effects of a wide range of environmental stresses, including starvation, predation, parasitism, and competition (13). Thus, parental care may indirectly buffer against inbreeding depression by alleviating these stresses (14), but currently there is little empirical evidence in support of this suggestion. A study on a subsocial spider (*Anelosimus cf. jucundus*, currently *Anelosimus arizona*) proposed that the absence of detectable inbreeding depression in

the offspring of this species could be caused by the buffering effects of either parental care or group living (14). The only experimental test of this hypothesis, conducted on the European earwig (*Forficula auricularia*), found no evidence that maternal care reduced the fitness costs of inbreeding depression (9).

Here, we tested whether parental care can buffer against inbreeding depression in the burying beetle *Nicrophorus vespilloides*, an insect with facultative parental care. Although there is no prior information on the effect of the interaction between parental care and the offspring’s inbreeding status, the independent effects of parental care and inbreeding status on offspring fitness are well established in this species (15, 16). Parental removal experiments show that larval growth is reduced if the caring parents are removed during the early stages of development when offspring are too young to self-feed efficiently (15). Furthermore, inbred offspring suffer reduced survival at the larval stage (16).

To test for a causal effect of parental care on the severity of inbreeding depression, we used a  $2 \times 2$  factorial design with the following factors: (i) presence or absence of posthatching maternal care and (ii) inbred or outbred offspring. All parents used in this experiment were outbred. Because inbreeding depression can affect traits across the entire life cycle of an organism, we assessed the joint effects of inbreeding status and maternal care on the following fitness-related offspring traits: (i) time to dispersal from the carcass (corresponding to the end of the parental care period); (ii) larval survival to dispersal; (iii) average larval mass at the time of dispersal; (iv) survival from dispersal to eclosion as an adult; and (v) posteclosion lifespan. We predicted that if maternal care can buffer against inbreeding depression, the presence of the mother would have a stronger fitness effect on inbred offspring than on outbred offspring.

## Significance

When relatives mate, their inbred offspring often suffer a reduction in fitness-related traits known as “inbreeding depression.” Environmental stresses such as starvation and competition can exacerbate these fitness costs of inbreeding. However, caring parents could mitigate the fitness costs of inbreeding by neutralizing the effects of these environmental stresses. We tested the hypothesis that maternal care can buffer against inbreeding depression in the offspring in burying beetles. Indeed, the female’s presence led to a higher increase in larval survival in inbred than in outbred broods, and it increased the lifespan of inbred but not outbred adults. Our findings suggest that parental care can moderate the severity of inbreeding depression, possibly affecting how parental care strategies and inbreeding avoidance mechanisms evolve.

Author contributions: N.P. and P.T.S. designed research; N.P. and S.J. performed research; N.P. and J.A.M. analyzed data; and N.P., J.A.M., and P.T.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence may be addressed. Email: n.pilakouta@gmail.com or per.t.smiseth@ed.ac.uk.

## Results

Maternal care shortened the time to dispersal from the carcass, but there was no difference in time to dispersal between inbred and outbred broods, and there was no effect of the interaction between maternal care and the offspring's inbreeding status (Tables 1 and 2). Time to dispersal was significantly shorter when the female parent was younger (estimate = 0.038 d, SE = 0.008,  $t_{84} = 4.87$ ,  $P < 0.0001$ ). Finally, there was no effect of carcass size ( $t_{84} = 1.21$ ,  $P = 0.23$ ) or the number of larvae dispersing ( $t_{84} = -0.127$ ,  $P = 0.90$ ) on time to dispersal.

Maternal care significantly increased the probability that at least one larva in a brood survived to dispersal (zero hurdle model: estimate = 0.964, SE = 0.241,  $z_{84} = 4.00$ ,  $P < 0.0001$ ). The offspring's inbreeding status did not have a significant effect on this component of larval survival (zero hurdle model:  $z_{84} = 1.91$ ,  $P = 0.056$ ), and there was no effect of the interaction between maternal care and inbreeding status (zero hurdle model:  $z_{84} = 1.09$ ,  $P = 0.28$ ). For broods in which at least one larva was present at dispersal, both maternal care and offspring inbreeding status had an effect on larval survival (Tables 1 and 2). The interaction between these two factors also had a significant effect (Table 1), because maternal presence improved the survival of inbred larvae more than that of outbred larvae (Table 2). There were no detectable effects of carcass size ( $z_{84} = -0.62$ ,  $P = 0.54$ ) or female age ( $z_{84} = 1.77$ ,  $P = 0.076$ ) on larval survival to dispersal.

Maternal care significantly increased larval mass at dispersal, but there was no significant effect of inbreeding status on larval mass and no significant interaction between maternal care and inbreeding status (Tables 1 and 2). Furthermore, larval mass did not depend on carcass size ( $t_{84} = -0.15$ ,  $P = 0.88$ ) or female age ( $t_{84} = -1.08$ ,  $P = 0.28$ ).

Both maternal care and inbreeding status had significant effects on the offspring's survival to eclosion. Maternal care increased survival to eclosion, and outbred larvae had higher survival than inbred ones (Tables 1 and 2). Survival to eclosion was not influenced by the interaction between maternal care and inbreeding status (Table 1).

Last, maternal care increased the lifespan of offspring after eclosion, and outbred offspring had longer lifespans than inbred ones (Tables 1 and 2). The statistically significant interaction between inbreeding status and maternal care indicated that receiving care improved the lifespan of inbred adults but not of outbred adults (Tables 1 and 2). There was no evidence for a difference in lifespan after eclosion between males and females ( $z_{448} = -0.33$ ,  $P = 0.74$ ).

Overall, we found evidence for inbreeding depression in survival to dispersal, survival from dispersal to eclosion, and lifespan after eclosion (Table 1). Moreover, we found evidence for a significant interaction between maternal care and offspring inbreeding status for survival to dispersal and posteclosion lifespan,

indicating a buffering effect of maternal care (Table 1). This conclusion is supported by our estimates of inbreeding depression ( $\delta$ ), which show that maternal care moderates the severity of inbreeding depression in these two traits (Fig. 1 and Table 2).

## Discussion

We provide experimental evidence supporting the suggestion that parental care can buffer against the deleterious effects of inbreeding on offspring fitness (14). First, we found that maternal care had a greater positive effect on larval survival to dispersal in inbred broods than in outbred broods. Second, we found that maternal care increased the lifespan of inbred offspring but not of outbred offspring. Thus, our results show that the buffering effects of parental care are detectable not only during the period when offspring depend on parental care (i.e., from egg laying to dispersal from the carcass) but also later in life when offspring have become independent. To our knowledge, this is the first study to show a causal effect of parental care on the severity of inbreeding depression. We provide a more detailed discussion of our results below.

Our first key finding was that maternal care had a stronger effect on survival to dispersal in inbred than in outbred larvae. This finding provides clear evidence that maternal care buffers against inbreeding depression during the period when larvae depend on maternal care. Before independence, larvae benefit directly from various components of maternal care, such as food provisioning (16, 17), defense against conspecific intruders (18), and defense against bacterial and fungal competitors through antimicrobial secretions (19). Thus, during this period, caring parents are in a position to neutralize directly the negative effects of the environmental stresses that are otherwise expected to exacerbate the fitness costs of inbreeding depression (11, 12).

Our second key finding was that maternal care increased the adult lifespan of inbred offspring but not of outbred offspring. This finding shows that parental care can buffer against inbreeding depression in offspring long after they have become independent of their parents. The extended adult lifespan of inbred offspring resulting from maternal care may indicate that maternal care increases the general condition of inbred offspring, thereby enhancing their survival prospects after the end of the parental care period. Our results show that the buffering effects of parental care against inbreeding depression can occur across different life stages, reinforcing the importance of measuring fitness consequences across an individual's whole life span (6).

Our finding that maternal care in *N. vespilloides* buffers against inbreeding depression in larval survival and adult lifespan contrasts with a recent study that found no evidence for a buffering effect on larval survival in the European earwig (9). One potential explanation for these opposing results is that no inbreeding depression in larval survival was observed in European

**Table 1. Effects of maternal care and offspring inbreeding status on fitness-related offspring traits**

Offspring trait	Maternal care				Inbreeding status				Interaction			
	Est	SE	z/t	P	Est	SE	z/t	P	Est	SE	z/t	P
Time to dispersal	-1.00	0.25	-4.0	<b>&lt;0.001</b>	0.26	0.41	0.64	0.52	-0.64	0.51	-1.3	0.21
Survival to dispersal	0.67	0.10	6.8	<b>&lt;0.0001</b>	0.77	0.10	7.6	<b>&lt;0.0001</b>	-0.49	0.12	-4.2	<b>&lt;0.0001</b>
Larval mass	0.027	0.008	3.5	<b>&lt;0.001</b>	0.006	0.007	0.85	0.40	0.011	0.011	1.0	0.31
Survival to eclosion	1.22	0.41	3.0	<b>0.004</b>	1.88	0.50	3.7	<b>&lt;0.001</b>	-0.12	0.80	-0.15	0.88
Posteclosion lifespan	0.53	0.09	5.8	<b>&lt;0.0001</b>	0.36	0.09	4.2	<b>&lt;0.0001</b>	-0.53	0.11	-4.8	<b>&lt;0.0001</b>

We provide information on the parameter estimates (Est), SEs, test statistics ( $z$  and  $t$  values), and  $P$  values for time to dispersal (days), larval survival to dispersal (%), larval mass (grams), survival from dispersal to eclosion (%), and posteclosion lifespan (days). The data were analyzed using general linear models for time to dispersal and larval mass and generalized linear models for survival to eclosion (fitted with a quasibinomial error structure) and lifespan (fitted with a negative binomial error structure). We used a ZAP regression to analyze the zero-inflated data on survival to dispersal, and here we present the results for the count model (see text for zero-hurdle model results). Statistically significant  $P$  values are indicated in bold.





care may facilitate the evolution of inbred social systems by reducing the fitness costs of inbreeding depression associated with such a transition. Nevertheless, the argument by Avilés and Bukowski (14) implicitly assumes that parental care itself is not subject to inbreeding depression. Theoretical considerations suggest that this assumption might be violated (24, 25), in which case persistent inbreeding might affect the parents' ability to buffer against inbreeding depression in their offspring. Given these theoretical predictions and some mixed evidence from empirical studies on the effect of inbreeding on parental care (26–28), we encourage further work in this area.

Based on our findings, we expect selection for inbreeding avoidance to be relaxed when parental care can moderate the deleterious effects of inbreeding in the offspring (provided that parental care itself is not subject to inbreeding depression). Under these conditions, the buffering effects of parental care may favor inbreeding tolerance or even inbreeding preference, a possibility that has been overlooked in the literature. Theoretical models emphasize the importance of the costs of dispersal, mating system, mate encounter rate, and kin recognition as important factors shaping the balance between inbreeding tolerance and avoidance (29–31). To our knowledge, the only theoretical study to specifically consider the role of parental care concludes that biparental care should lead to lower inbreeding tolerance, because both parents must put in a substantial amount of parental effort for a relatively small return in the form of inbred offspring (30). However, existing theory has not considered that parental care might moderate the severity of inbreeding depression in the offspring, in which case it could have the opposite effect of leading to higher inbreeding tolerance. For example, in an African cichlid with biparental care (*Pelvicachromis taeniatus*), both sexes preferentially mate with a close relative (32). There is no evidence for inbreeding depression in this species, and it has been suggested that the absence of inbreeding depression results from the occurrence of parental care (9, 32). The buffering effects of parental care on offspring fitness may interact with life-history traits and mating dynamics to determine an organism's inbreeding strategy, which in turn can have profound implications for the maintenance of genetic variation within a population (5, 6). Considering the wider implications of the potential effects of parental care on the severity of inbreeding depression may thus help us better understand and predict when animals should avoid, tolerate, or prefer inbreeding (5).

In summary, our findings have important implications for the understanding of inbreeding, a central topic in ecology and evolutionary biology. First, we show that the buffering effects of parental care were detectable not only during the period when larvae depend on parental care (i.e., from egg laying to dispersal from the carcass) but also long after independence. We expect such buffering to be widespread in species with parental care, even in populations with no history of inbreeding, as long as parental care can alleviate environmental stress and kin matings lead to considerable inbreeding depression in the offspring. Second, the buffering effects of parental care may favor the evolution of inbred mating systems or inbreeding tolerance by reducing the fitness costs to inbred offspring (14). Therefore, a better understanding of how parental care and other forms of sociality can influence the expression of inbreeding depression may help explain the observed variation in animal inbreeding strategies.

## Materials and Methods

**Study Species.** Burying beetles (*N. vespilloides*) breed on carcasses of small vertebrates and have facultative biparental care. Parents bury the carcass in the soil and lay the eggs around it (33). They prepare the carcass by removing any fur or feathers and apply antimicrobial secretions to suppress bacterial and fungal growth (33, 34). After hatching, larvae crawl to the carcass and start feeding in a crater created by the parents. The larvae can self-feed, but parents also provision larvae with predigested carrion (16). In addition, parents defend

the brood from predators and conspecific competitors (35). The larvae disperse from the carcass about 5 d after hatching, pupate about 10 d after dispersal, and eclose as adults about 10 d after pupation.

**Experimental Design.** We used beetles from an outbred laboratory population maintained at The University of Edinburgh. To avoid inbreeding in the stock population, we maintained a large population (500–1,000 individuals per generation) and mated only unrelated or distantly related individuals (i.e., no common ancestors for at least two generations). The beetles used in this study comprised of third- and fourth-generation beetles from lines originally collected in Edinburgh and Warmond, The Netherlands. Similar numbers of beetles were used from each line, and there was no evidence of outbreeding depression. They were housed individually in transparent plastic containers ( $12 \times 8 \times 2$  cm) filled with moist soil and kept at 20 °C and constant light. Nonbreeding adults were fed raw organic beef twice a week.

To examine whether parental care buffers against inbreeding depression, we used a  $2 \times 2$  factorial design with the following treatment groups: (i) outbred offspring that received maternal care ( $n = 32$ ); (ii) outbred offspring that received no maternal care ( $n = 33$ ); (iii) inbred offspring that received maternal care ( $n = 33$ ); and (iv) inbred offspring that received no maternal care ( $n = 33$ ). To produce outbred offspring for treatment groups 1 and 2, we paired outbred virgin beetles that did not share ancestors for at least two generations. To produce inbred offspring for treatment groups 3 and 4, we paired outbred virgin beetles that were full siblings. These experimental pairs ( $n = 131$ ) were randomly assigned to treatments (care or no care). They then were transferred to transparent plastic containers ( $17 \times 12 \times 6$  cm) filled with 1 cm of moist soil and provided with a previously frozen mouse carcass (Livefoods Direct Ltd.) of a standardized size (24–27 g). In this species, the amount of care provided by the male is highly variable, and male removal has no average effect on offspring fitness under laboratory conditions (36). For this reason, we removed males from all treatments after eggs were laid but before the larvae had hatched. In treatment groups 2 and 4, we also removed females at the same time, but females were left to care for their brood until dispersal in treatment groups 1 and 3.

When all larvae had dispersed from the carcass, we recorded the date, the number of surviving larvae, and the total mass of the brood. These data were used to calculate time to dispersal and average larval mass for each brood. All larvae, up to a maximum of 15 per brood, were placed into large transparent boxes filled with moist soil. At eclosion, we recorded the proportion of individuals that eclosed successfully from each brood and placed up to six beetles into individual containers. We tracked the mortality of these beetles ( $n = 449$ ) by checking them twice a week until death.

**Statistical Analyses.** All data were analyzed using R version 3.1.1. We used general linear models for traits that had a normal error structure (average larval mass and time to dispersal). For survival to eclosion, we used a generalized linear model fitted with a quasibinomial error distribution, and for posteclosion lifespan we used a generalized linear model fitted with a negative binomial error distribution. Because of a high proportion of zeros in the larval survival data, we ran a zero-adjusted Poisson (ZAP) regression using the hurdle function in the pscl package (37). A Poisson structure was assumed for the count model, and a binomial structure was assumed for the zero-hurdle model. Significant values on the count model indicate that a given variable had an effect on the number of larvae surviving to dispersal, whereas significant values on the zero-hurdle model indicate that a given variable had an effect on the probability of having zero versus nonzero larvae at dispersal.

All models included parental care (maternal presence or absence) and inbreeding status (inbred or outbred offspring) as main effects, as well as an interaction between these two factors. Carcass size was included as an additional covariate in the models for time to dispersal, survival to dispersal, and average larval mass, because the amount of resources available may influence offspring growth and survival. We also added female age to the models for time to dispersal, survival to dispersal, and average larval mass, because the amount of care a female provides may depend on her age. Note that there was no significant difference in female age between treatments [one-way ANOVA;  $F(3,127) = 0.26$ ,  $P = 0.86$ ]. Last, we added sex as a factor in the lifespan model because of the possibility of sex-specific mortality (38). Decisions as to which variables to include in the final model were based on Akaike Information Criterion model-selection criteria.

To compare inbreeding depression in offspring fitness traits between the care and no care treatments, we calculated inbreeding depression as a proportional change in mean fitness of outbred ( $w_o$ ) and inbred offspring ( $w_i$ ) based on the equation  $\delta = (w_o - w_i)/w_o$  (Table 2) (39).

**ACKNOWLEDGMENTS.** We thank the Edinburgh Countryside Rangers for permission to collect beetles at Corstorphine Hill, Daniel Rozen for supplying beetles from The Netherlands, Charlotte Regan for suggestions on the statistical

analyses, Maarit Mäenpää and Ashleigh Whiffin for assistance in maintaining the laboratory population, and three anonymous reviewers for helpful comments on the manuscript.

- Charlesworth D (2003) Effects of inbreeding on the genetic diversity of populations. *Philos Trans R Soc Lond B Biol Sci* 358(1434):1051–1070.
- Charlesworth D, Willis JH (2009) The genetics of inbreeding depression. *Nat Rev Genet* 10(11):783–796.
- Escobar JS, et al. (2011) Patterns of mating-system evolution in hermaphroditic animals: Correlations among selfing rate, inbreeding depression, and the timing of reproduction. *Evolution* 65(5):1233–1253.
- Liu XH, Yue LF, Wang W, Li N, Cong L (2013) Inbreeding avoidance drives consistent variation of fine-scale genetic structure caused by dispersal in the seasonal mating system of Brandt's voles. *PLoS ONE* 8(3):e58101.
- Szulkin M, Stopher KV, Pemberton JM, Reid JM (2013) Inbreeding avoidance, tolerance, or preference in animals? *Trends Ecol Evol* 28(4):205–211.
- Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annu Rev Ecol Syst* 18:237–268.
- Crnokrak P, Roff DA (1999) Inbreeding depression in the wild. *Heredity (Edinb)* 83(Pt 3):260–270.
- Keller L, Waller D (2002) Inbreeding effects in wild populations. *Trends Ecol Evol* 17(5):230–241.
- Meunier J, Kölliker M (2013) Inbreeding depression in an insect with maternal care: Influences of family interactions, life stage and offspring sex. *J Evol Biol* 26(10):2209–2220.
- Moorad JA, Wade MJ (2005) A genetic interpretation of the variation in inbreeding depression. *Genetics* 170(3):1373–1384.
- Fox CW, Reed DH (2011) Inbreeding depression increases with environmental stress: An experimental study and meta-analysis. *Evolution* 65(1):246–258.
- Reed DH, Fox CW, Enders LS, Kristensen TN (2012) Inbreeding-stress interactions: Evolutionary and conservation consequences. *Ann N Y Acad Sci* 1256:33–48.
- Royle NJ, Smiseth PT, Kölliker M (2012) *The Evolution of Parental Care* (Oxford Univ Press, Oxford).
- Avilés L, Bukowski TC (2006) Group living and inbreeding depression in a subsocial spider. *Proc Biol Sci* 273(1583):157–163.
- Smiseth PT, Darwell CT, Moore AJ (2003) Partial begging: An empirical model for the early evolution of offspring signalling. *Proc Biol Sci* 270(1526):1773–1777.
- Mattey SN, Strutt L, Smiseth PT (2013) Intergenerational effects of inbreeding in *Nicrophorus vespilloides*: Offspring suffer fitness costs when either they or their parents are inbred. *J Evol Biol* 26(4):843–853.
- Eggert Ak, Reinking M, Müller JK (1998) Parental care improves offspring survival and growth in burying beetles. *Anim Behav* 55(1):97–107.
- Trumbo ST (2007) Defending young biparentally: Female risk-taking with and without a male in the burying beetle, *Nicrophorus pustulatus*. *Behav Ecol Sociobiol* 61(11):1717–1723.
- Arce AN, Johnston PR, Smiseth PT, Rozen DE (2012) Mechanisms and fitness effects of antibacterial defences in a carrion beetle. *J Evol Biol* 25(5):930–937.
- Bulmer MG (1973) Inbreeding in the great tit. *Heredity (Edinb)* 30(3):313–325.
- Walling CA, et al. (2011) Inbreeding depression in red deer calves. *BMC Evol Biol* 11:318.
- Tallamy DW, Wood TK (1986) Convergence patterns in subsocial insects. *Annu Rev Entomol* 31:369–390.
- Avilés L, Purcell J (2012) The evolution of inbred social systems in spiders and other organisms: From short-term gains to long-term evolutionary dead ends? *Adv Stud Behav* 44:99–133.
- Linksvayer TA, Wade MJ (2009) Genes with social effects are expected to harbor more sequence variation within and between species. *Evolution* 63(7):1685–1696.
- Falconer DS, Mackay TFC (1996) *Introduction to Quantitative Genetics* (Longman, Essex, UK).
- Pooley EL, Kennedy MG, Nager RG (2014) Maternal inbreeding reduces parental care in the zebra finch, *Taeniopygia guttata*. *Anim Behav* 97:153–163.
- Margulis SW (1998) Relationships among parental inbreeding, parental behaviour and offspring viability in oldfield mice. *Anim Behav* 55(2):427–438.
- Mattey SN, Smiseth PT (2015) Complex effects of inbreeding on biparental co-operation. *Am Nat* 185(1):1–12.
- Waser PM, Austad SN, Keane B (1986) When should animals tolerate inbreeding? *Am Nat* 128(4):529–537.
- Kokko H, Ots I (2006) When not to avoid inbreeding. *Evolution* 60(3):467–475.
- Lehmann L, Perrin N (2003) Inbreeding avoidance through kin recognition: Choosy females boost male dispersal. *Am Nat* 162(5):638–652.
- Thünken T, Bakker TCM, Baldauf SA, Kullmann H (2007) Active inbreeding in a cichlid fish and its adaptive significance. *Curr Biol* 17(3):225–229.
- Scott MP (1998) The ecology and behavior of burying beetles. *Annu Rev Entomol* 43:595–618.
- Eggert A-K (1992) Alternative male mate-finding tactics in burying beetles. *Behav Ecol* 3(3):243–254.
- Smiseth PT, Moore AJ (2004) Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behav Ecol* 15(4):621–628.
- Smiseth PT, Dawson C, Varley E, Moore AJ (2005) How do caring parents respond to mate loss? Differential response by males and females. *Anim Behav* 69(3):551–559.
- Jackman S (2014) pscl: Classes and methods for R developed in the Political Science Computational Laboratory, Stanford University. R package version 1.4.6. Available at [pscl.stanford.edu/](http://pscl.stanford.edu/). Accessed November 18, 2014.
- Fox CW, et al. (2006) The genetic architecture of life span and mortality rates: gender and species differences in inbreeding load of two seed-feeding beetles. *Genetics* 174(2):763–773.
- Hedrick PW, Kalinowski ST (2000) Inbreeding depression in conservation biology. *Annu Rev Ecol Syst* 31:139–162.